GERMINATION OF *XANTHORRHOEA AUSTRALIS* USING TREATMENTS THAT MIMIC POST-FIRE AND UNBURNT CONDITIONS

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CURTIS, N. P., 2001:12:17. Germination of *Xanthorrhoea australis* using treatments that mimic post-fire and unburnt conditions. *Proceedings of the Royal Society of Victoria* 113(2): 237–245. ISSN 0035-9211.

Seed germination, using two different-aged seed batches of *Xanthorrhoea australis* Robert Brown, was carried out in growth cabinet trials using (i) treatments that mimic conditions of soils with a high charcoal content found after fire-stimulated flowering and (ii) on soils with little charcoal content and carrying ground cover which lessens light intensity, being conditions found after infrequent flowering that occurs without fire stimulation. Treatments were powdered charcoal, charcoal filtrate, gibberellic acid and differing light intensities. After 54 days, there was no significant difference ($P > 0.05$) in the number of germinants for each treatment, but in each treatment there were significant differences in the time taken to commence germination and the rate of germination. In full light, seeds stored for five years in paper bags at room temperature, germinated earlier than the seeds stored in the same way for one year ($P < 0.05$) at day 15. The difference was significant at day 18 with charcoal powder and light ($P < 0.01$) and also at day 15 in darkness ($P < 0.001$). Germination in light and charcoal filtrate was faster ($P < 0.05$ at day 18). In light reduced by a filter to 25% of the full intensity, seeds germinated earlier than those in brighter light ($P < 0.05$) at day 15, but not as early as seeds in darkness. Germination in the presence of gibberellic acid was faster in both light and darkness ($P < 0.001$) at day 21 and maximum germination was attained earlier than in other treatments. The results provide useful information on the management of *X. australis*, suggesting that seed may be stored for long periods and there is a beneficial effect when germination occurs under understorey species which later protect germinants from grazing.

Key words: cabinet trials, seed germination, *Xanthorrhoea australis*, charcoal, light variation.

THE spectacular post-fire flowering response of *Xanthorrhoea australis* is accepted as an adaptive response to fire. Many authors have recorded this phenomena (Willis 1970; Gill & Ingwersen 1976; Gill 1981; Gill & Groves 1981; Staff 1989). However, the species will also flower sporadically in the inter-fire period (Gill & Ingwersen 1976; Gill & Groves 1981; Staff 1989; Curtis 1996, 1998). Flowering in *X. australis* occurs early in the spring (August–September) when a large inflorescence may produce 1700–10 000 seeds (Staff 1975; Gill 1981). The following autumn, most of the seeds will be shed, but some will remain on the flower spike through the winter and will be shed the following spring or later (Curtis 1993, 1996). The sites used for germination field trials were in fenced areas 25 m square which provided different substrates and protection from grazing. In these sites very few surface sown seeds germinated and survived, whereas germinants of seeds buried to a depth of 3 mm had a survival rate of 27–42% (Curtis 1993, 1996).

The consequence of post-fire and sporadic inter-fire flowering is that the seeds are dispersed onto two different substrates. In the Mediterranean climate of north-east Victoria, natural fire events usually occur in the summer whilst prescribed burning is usually carried out in the autumn. As a consequence *X. australis* seeds fall 12 or 18 months after the fire onto soil carrying very little ground cover and a large amount of charcoal which has been leached by autumn and winter rainfall. When flowering occurs without fire stimulus, seeds fall onto soil which incorporates little charcoal and carries moss species, small plants, herbs and grasses and leaf litter (Curtis 1996) and an environment where the light intensity is probably lower. It was observed that in these sites *X. australis* seedlings were mainly growing in the protection of *Brachyloma daphnoides* (vascular plant nomenclature of Victorian species follow Ross 2000), a species widely distributed throughout the Warby Range State Park (Curtis 1993; Curtis 1996; Curtis 1998).

Prior to the research of Curtis (1993, 1996), there was no published research on the seed ecology and the early establishment of *X. australis*. However, Western Australian members of this genus are better studied (Bellairs & Bell 1990; Bell 1994; Bell et al. 1995), including the effect of gibberellic acid on some species. These, and the study of an eastern member of the genus, *X. johnsonii* (Peterson 1987), provided a background for the studies of Curtis (1993, 1996).

The results of Curtis (1993, 1996) showed that in growth cabinets, germination of *X. australis* seed harvested in the Warby Range State Park, was affected by temperature, light, stratification, and the time of seed picking. The optimum temperature for germination of 15–20°C in the laboratory matched field conditions during times of reliable rainfall in the Warby Range State Park. However, seeds kept in a diurnal alternating temperature of 12–20°C, or planted in the field in autumn, germinated six weeks earlier than those under a fixed temperature regime. Secondary dormancy was induced at 30°C and seven weeks later when the temperature was lowered to 20°C, the germination was significantly greater in darkness. Germination was greatly accelerated by the absence of light and by stratification at 4°C for 11 weeks. The time of seed harvest affected germination, with spring-picked seeds germinating significantly earlier than autumn-picked seeds, both seed types being picked in the same year.

Although the research provided information of the germination ecology of *X. australis*, it left many unanswered questions. Seeds produced in the same season that were picked later (in the spring), were found to be more responsive to darkness than seeds picked earlier (autumn). Would this response to darkness be similar in seeds that had been stored for a longer time? The presence of compounds produced after the wood of Californian chaparral species was heated to 175°C for 30 minutes increased germination (Keeley et al. 1985; Keeley & Pizzorno 1986). Curtis (1993, 1996) also found in laboratory and field trials in fenced plots that germination of *X. australis* seeds was earlier and more rapid in the presence of charcoal which darkened the surface of the substrate. Was this effect in *X. australis* seeds due to the darker soil color causing beneficial temperature differences, or chemicals associated with the charcoal? Would the presence of gibberellic acid cause earlier and more rapid germination in *X. australis* as it did in Western Australian members of the genus?

This study aims to determine the effect of (i) long-term storage of seeds, (ii) the presence of charcoal in a solid state, (iii) a solution made from a filtered suspension of charcoal powder in water, (iv) different light intensities and (v) gibberellic acid on the germination of *X. australis*.

MATERIALS AND METHODS

Seed collection

Xanthorrhoea australis seeds harvested in autumn (March–April) 1992 from a flowering in spring 1991 (five-year-old seed), were stored at room temperature and humidity, in sealed brown paper bags without added insecticide. Seeds harvested in the autumn of 1996 from a flowering in spring 1995 (one-year-old seed) were stored in the same way and used for all but one of the experiments. After each harvesting, the seed from at least 15 *X. australis* were mixed and before sowing, the seeds were inspected for damage or larval attack and any suspect seeds were rejected.

Laboratory trials

In March 1997, carbonised leaf bases from burnt *X. australis* plants were collected from the soil surface of an area in the Warby Range State Park, prescribed burnt in March 1996. At the time of collection, the carbonised leaf bases would have been subjected to the leaching effect of winter and spring rains which are the conditions in which *X. australis* seed germinate after prescribed burning the previous autumn. Three days later these were ground into a fine powder with a pestle and mortar, and 200 g of sieved charcoal powder was mixed in 500 ml of autoclaved distilled water. After mechanical agitation for 20 minutes, the solution was filtered and stored at 4°C. Another treatment used powdered charcoal sieved through a fine mesh to remove larger particles. The seeds were sown on previously autoclaved paper and imbibed with 10 ml of sterile distilled water. After sprinkling carbon powder over the seeds and paper, a further 3 ml of water was added.

In the differential light experiments, sheets of photographic neutral grey filter that completely covered the tray containing the petri dishes, were taped to the edge of the tray to exclude extraneous light from the petri dishes. Treatments used were: no filter (100% light), one layer (reducing the light to 50%), two layers (reducing the light to 25%) and 3 layers (reducing the light to 12.5%).

For each treatment, 10 seeds were sown in pre-sterilised plastic petri dishes on Whatman No. 182 seed test paper that had been previously autoclaved for 20 minutes at 121°C at 10^5 Newtons^2 (15 psi) pressure. There were five replicates of each treatment. After sowing, the seeds were imbibed with 9 ml of autoclaved distilled water, the exceptions being the experiments using gibberellic acid and charcoal filtrate. A treatment using 9 ml of gibberellic acid (GA_3, 50 mg/L), were sown and continued for 54 days. The petri dishes were sealed with NescoFilm (Nippon Shoji Kaisaha Ltd, Osaka, Japan) tape and placed on opaque trays on the same cabinet shelf. At times of counting germinants, water was added where necessary to ensure complete imbibition and the dishes resealed.

The trials mimicked the conditions found in the Warby Range State Park, in spring and autumn when conditions are optimal for seed germination (Fig. 1). A temperature regime of 20°C day and 12°C night was used, with a regime of 12/12 h light/dark cycle and complete darkness. Limited cabinet availability restricted the choice to one temperature regime.

Germination occurred upon the emergence of the radicle. Cumulative totals of germinants were recorded each time data were collected. At the end of the trials, any ungerminated seeds were cut and examined for apparent viability (judged on the basis that the embryo was intact and there was no cell degradation).

Field and cabinet light measurement

In order to determine the light intensities required for the cabinet trials, the amount of light reaching the soil was measured by determining the percentage of light availability under the ground cover plants in three sites: two flat fenced sites burnt in 1976 and 1991 (with ungrazed ground cover species) and an unfenced site unburnt for about 100 years which had a northerly aspect. All sites had an overstorey of mainly *Eucalyptus blakelyi* and *E. macrorhyncha*, and a ground cover of mainly *Brachyloma daphnoides* and grass species. Field data were taken on 7 June 1997 between 10.15 a.m. and 12.20 p.m. A Quantum Sensor which measured the photo flux in micromols of photons m^{-2} $second^{-1}$ ($\mu M\ m^{-2}\ s^{-1}$) photosynthetic radiation (PAR) was used. To ensure that no reflected light was received from the operator, the measuring receptor was taped to a 600 mm long

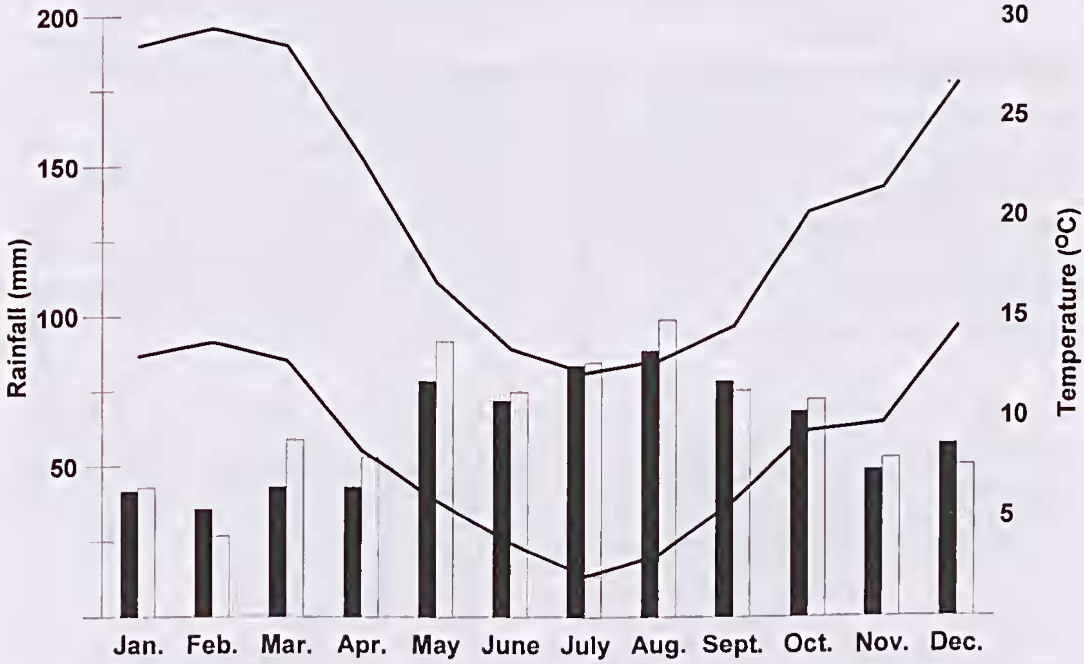

Fig. 1. Mean monthly rainfall at Wangaratta (dark bars) and Warby (light bars), and the mean monthly maxima and minima temperatures (continuous lines) at Wangaratta. Wangaratta data (Bureau of Meteorology, Melbourne), taken 16 km south-east of the study sites and Warby data (W. J. Wilson, Kala Rama, Wangandary, Victoria, 1975–1993) taken 6 km south-east of the study sites and at an altitude of 200 m (150 m lower than the study sites).

piece of unpainted wooden lath, 25 mm wide, held at arm's length. Forty measurements were taken with the receptor placed at ground level under the ground cover plants and at a height of 1 m above ground level. For all measurements, the receptor was kept parallel to the slope of the ground.

To measure photoflux levels in the cabinet trials, the receptor was placed with its top parallel to the shelf holding the seeds. Measurements were made with the doors closed and observations were made through a small observation window. Shelf measurements were the average of readings taken at 17 different points. Measurements of the photoflux under each of the light reducing filters were the average of three readings.

Statistical analysis

The number of seeds that germinated in each of the treatments was compared by one-way ANOVA using Minitab (Release 7; Minitab Inc. 1989); confidence intervals, where not expressed by Minitab, were calculated using tables published by Neave (1978). Statistical treatments mostly followed Fowler & Cohen (1990). Statistical calculations were based on the number of germinants and not the percentages.

RESULTS

Photoflux measurement

The average photoflux levels in the field sites below a ground-layer canopy was 10–51% of that found 1 m above the ground under the overstorey. In all sites there was a wide variation in all data (Table 1). The cabinet range of photoflux levels was 49–67 μM m^{-2} s^{-1} with an average of 58. In the differential light experiment the readings were: no filter (100% light) 63, one filter layer (50% light) 29, two filter layers (25% light) 14.5 and three filter layers (12.5% light) 6.75 μM m^{-2} s^{-1} (Table 2).

Light intensity	Average reading
Full light	58.4
50.0% light	29.0
25.0% light	14.5
12.5% light	6.75

Table 2. Photosynthetic Radiation (PAR) readings in growth cabinet, taken in full light on open shelf and under filters that reduce the light intensity to 50%, 25% and 12.5% of the full light. Shelf photoflux was average of 17 readings and photoflux under each light reducing filter was the average of three readings. Photoflux readings were measured in micromols m^{-2} second^{-1}.

Cabinet trials

Fifty-four days after commencing trials, storage, light, charcoal as a solid and filtrate, and gibberellic acid, had few detectable effects on the germination of *X. australis*. However, some minor trend differences in the breaking of dormancy and germination rates were observed (Figs 2–6).

The effect of storage on seeds had no significant effect on germination. Light broke dormancy faster in the earlier picked seeds than the later picked seeds, but in darkness the later picked seeds had more rapid germination (Fig. 2).

In light and the presence of charcoal powder, seeds broke dormancy three days earlier and had increased initial germination and number of germinations in the first three weeks. However, the overall effect was that untreated seeds had slightly better germination. In the dark, dormancy was broken earlier and germination was more rapid in the untreated seeds, but at day 54 both treatments had the same germination (Fig. 3).

Site fire history	Position of measuring receptor	Average photoflux reading	Maximum photoflux reading	Minimum photoflux reading
Burnt 1991	1.0 m above ground	228	690	40
	under ground cover plants	91	450	3
Burnt 1976	1.0 m above ground	162	700	10
	under ground cover plants	115	480	15
Unburnt	1.0 m above ground	286	470	50
	under ground cover plants	126	390	30

Table 1. Photosynthetic Radiation (PAR) readings taken in field sites in the Warby Range State Park, north-east Victoria, that underwent prescribed burning in 1991 and 1976 and an unburnt site. Readings were taken at ground level under ground cover plants and 1.0 m above ground level. Photoflux readings were the average of 40 readings taken on 7 June 1997 between 10.15 a.m. and 12.20 p.m., and were measured in micromols m^{-2} second^{-1}.

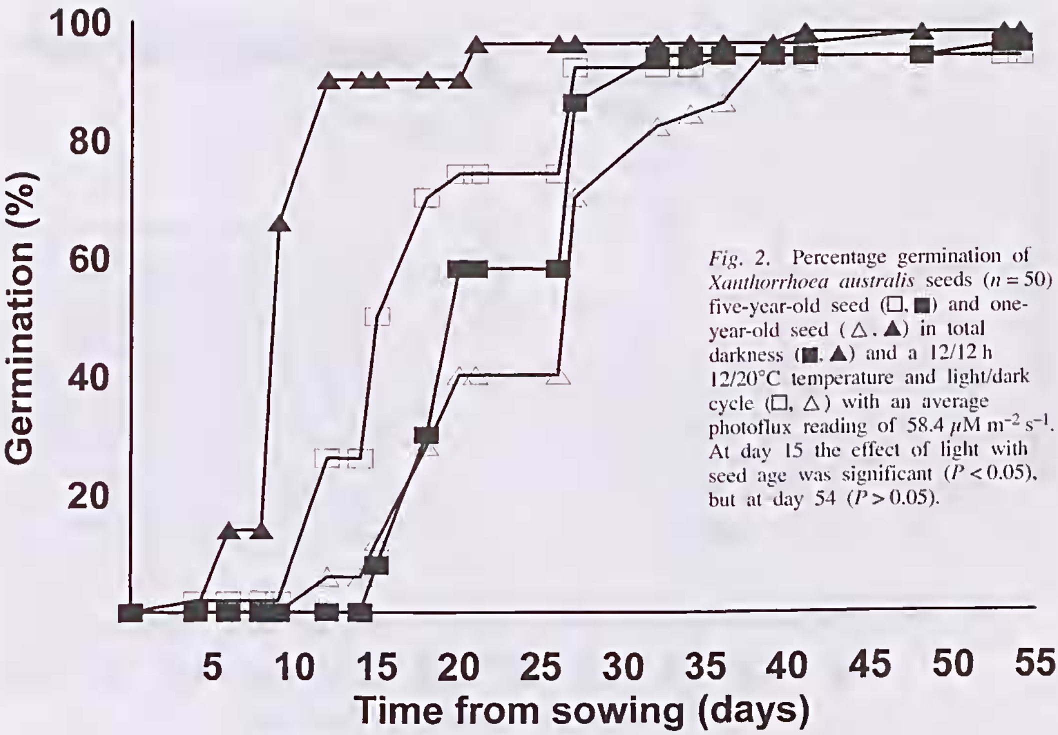

Fig. 2. Percentage germination of *Xanthorrhoea australis* seeds ($n = 50$) five-year-old seed (□, ■) and one-year-old seed (△, ▲) in total darkness (■, ▲) and a 12/12 h 12/20°C temperature and light/dark cycle (□, △) with an average photoflux reading of 58.4 μM m^{-2} s^{-1}. At day 15 the effect of light with seed age was significant ($P < 0.05$), but at day 54 ($P > 0.05$).

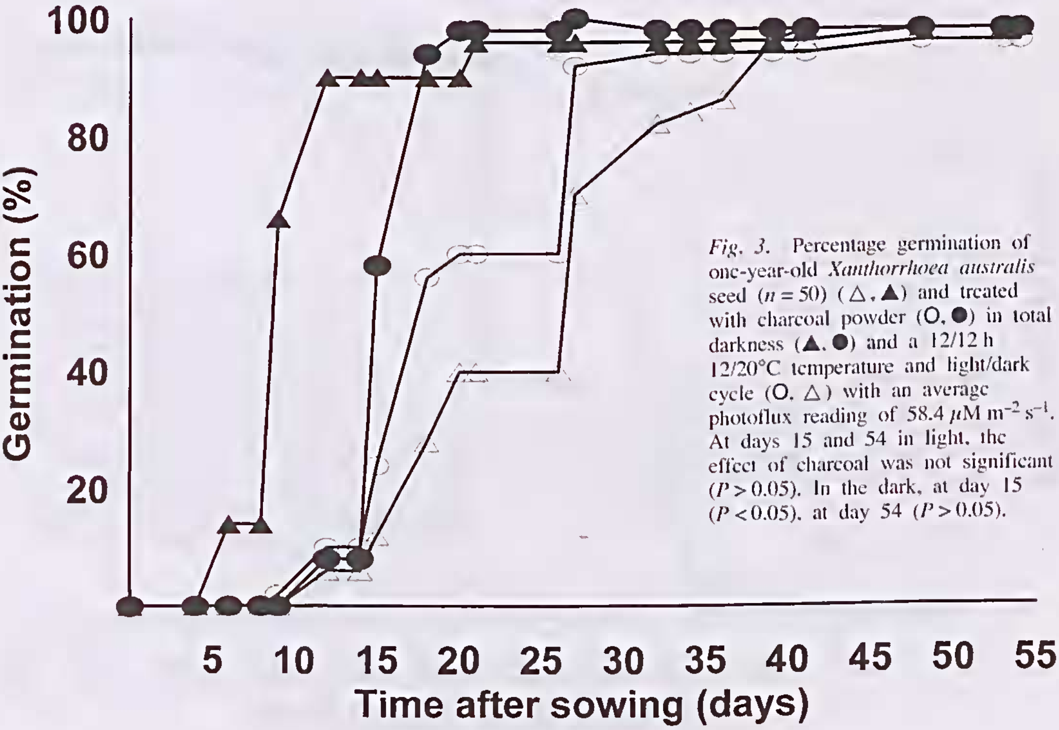

Fig. 3. Percentage germination of one-year-old *Xanthorrhoea australis* seed ($n = 50$) (△, ▲) and treated with charcoal powder (O, ●) in total darkness (▲, ●) and a 12/12 h 12/20°C temperature and light/dark cycle (O, △) with an average photoflux reading of 58.4 μM m^{-2} s^{-1}. At days 15 and 54 in light, the effect of charcoal was not significant ($P > 0.05$). In the dark, at day 15 ($P < 0.05$), at day 54 ($P > 0.05$).

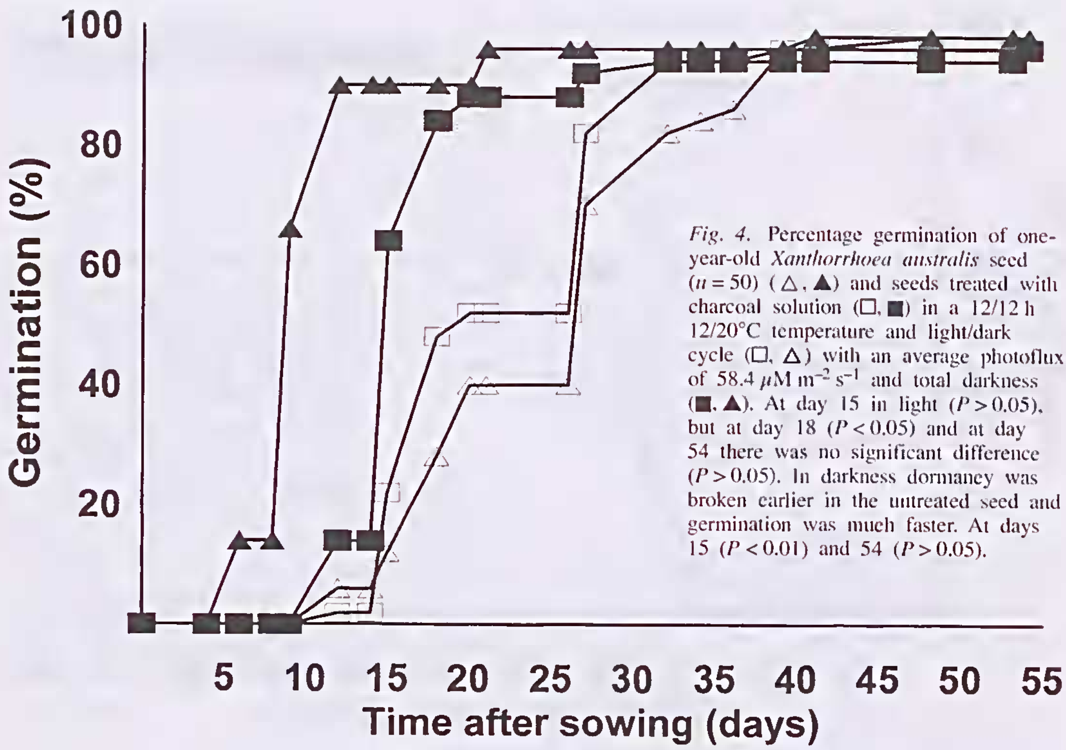

Fig. 4. Percentage germination of one-year-old *Xanthorrhoea australis* seed ($n = 50$) (△, ▲) and seeds treated with charcoal solution (□, ■) in a 12/12 h 12/20°C temperature and light/dark cycle (□, △) with an average photoflux of 58.4 μM m^{-2} s^{-1} and total darkness (■, ▲). At day 15 in light ($P > 0.05$), but at day 18 ($P < 0.05$) and at day 54 there was no significant difference ($P > 0.05$). In darkness dormancy was broken earlier in the untreated seed and germination was much faster. At days 15 ($P < 0.01$) and 54 ($P > 0.05$).

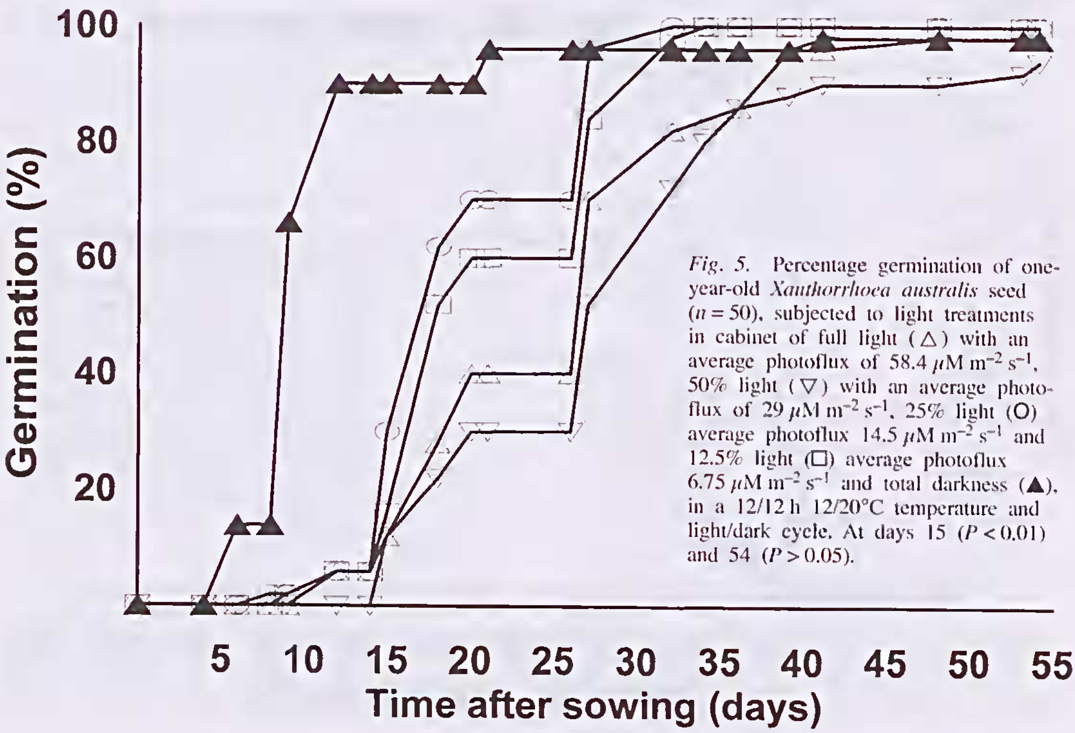

Fig. 5. Percentage germination of one-year-old *Xanthorrhoea australis* seed ($n = 50$), subjected to light treatments in cabinet of full light (△) with an average photoflux of 58.4 μM m^{-2} s^{-1}, 50% light (▽) with an average photoflux of 29 μM m^{-2} s^{-1}, 25% light (O) average photoflux 14.5 μM m^{-2} s^{-1} and 12.5% light (□) average photoflux 6.75 μM m^{-2} s^{-1} and total darkness (▲), in a 12/12 h 12/20°C temperature and light/dark cycle. At days 15 ($P < 0.01$) and 54 ($P > 0.05$).

Charcoal filtrate did not significantly reduce the time to break dormancy in light, but germination was more rapid than in the untreated seeds. In darkness, dormancy was broken five days earlier in the untreated seed and maximum germination was achieved earlier, but overall there was little difference between the treated and untreated seeds (Fig. 4).

Seeds germinating in the 25% light intensity broke dormancy earlier than in full light and the other light intensities, although not as early as seeds germinating in darkness. For about the first two weeks, the germination was greater in the 25% light, and commencement of germination of the seeds in the 50% light was delayed more than those in the 12.5%, 25% light and darkness, but overall none of the light treatments increased final germination significantly (Fig. 5).

In light and darkness, for the first two weeks, the presence of gibberellic acid had no significant effect on seed germination. However, a week later, seeds in a light regime had greater germination and reached a maximum of 98%, 21 days earlier than the untreated seeds. Because of cabinet problems, the experiment with GA_3 was terminated at day 27, when the treated seeds in the dark regime had 100% germination and it was not until day 40 that the untreated seeds in the dark regime had a similar germination rate (Fig. 6).

At the conclusion of the trials any ungerminated seeds were cut open and the embryo examined. In all of these the testa was found to be intact but the endosperm had decayed.

DISCUSSION

Flowering of *X. australis* in the absence of fire is spasmodic and irregular (Staff 1975; Curtis 1993, 1998). Fire-stimulated flowering results in a substantial seed crop that is available for germination the following autumn. The studies of Bellairs & Bell (1990), Bell et al. (1995), Curtis (1993, 1996), and the present study, have shown that there is little difficulty in germinating seeds of many species of the *Xanthorrhoea* genus. However, the key to successful longer-term regeneration of *X. australis* is the subsequent survival of germinants and seedlings (Curtis 1993, 1998).

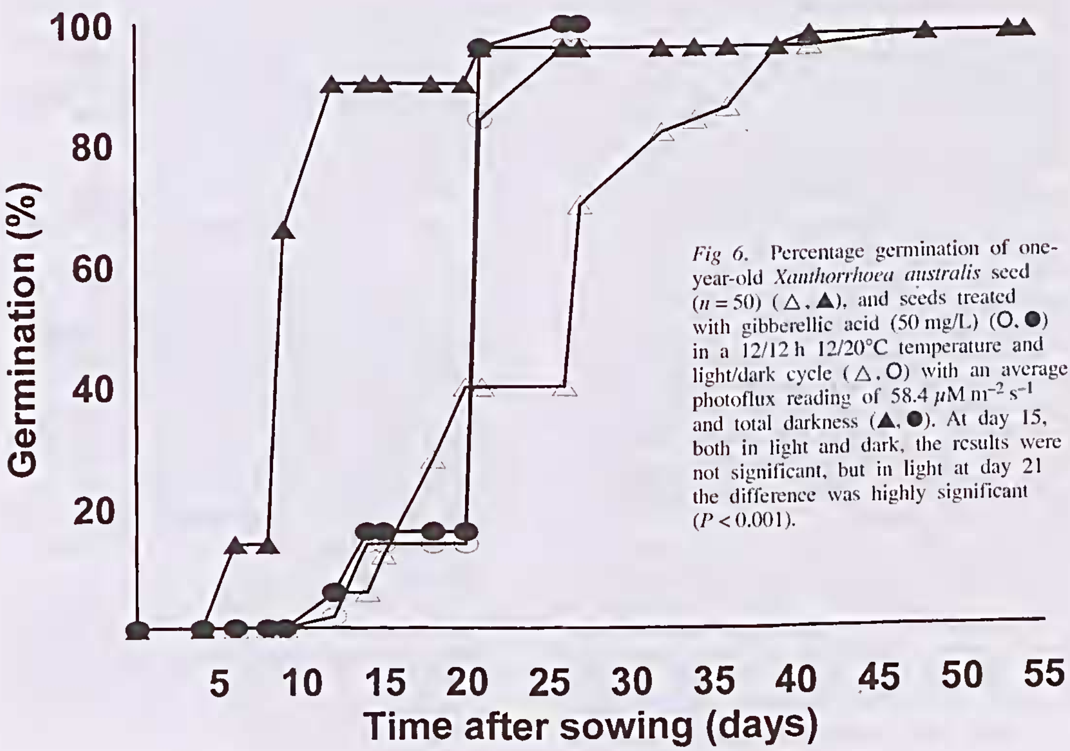

Fig 6. Percentage germination of one-year-old *Xanthorrhoea australis* seed ($n = 50$) (△, ▲), and seeds treated with gibberellic acid (50 mg/L) (O, ●) in a 12/12 h 12/20°C temperature and light/dark cycle (△, O) with an average photoflux reading of 58.4 μM m^{-2} s^{-1} and total darkness (▲, ●). At day 15, both in light and dark, the results were not significant, but in light at day 21 the difference was highly significant ($P < 0.001$).

It was found that young seeds germinate earlier and faster in total darkness, whereas old seeds germinate earlier and faster in light (Fig. 2). This suggests that a mixture of older and newer seeds would increase the number of germinants in areas requiring re-establishment of *X. australis*.

In controlled environment cabinet trials with *X. australis*, the presence of charcoal or charcoal filtrate affected dormancy of seed in light but not in darkness (Figs 3, 4). Carbonisation of material may not be necessary, because heating chaparral shrub material to 175°C for 30 minutes has produced water soluble compounds that stimulate germination (Keeley et al. 1985; Keeley & Pizzorno 1986). Alternatively, the charcoal from the burnt *X. australis* used in this study, may have been leached for about one year, lessening the effect of any (potential) stimulatory compound. Since germination in darkness was unaltered by the presence of charcoal, it would appear that any beneficial effect of charcoal may be due to the temperature advantage of the darker soil because of greater absorption of radiant heat from sunlight (Curtis 1993, 1996). In field trials on flat sites, Curtis (1993, 1996) found that *X. australis* seed buried 3 mm deep in soils darkened with charcoal after fire, germinated earlier and faster than in soils containing little or no charcoal. However, in this experiment no measurement of soil temperature by heat probes was done.

Curtis (1993, 1998) found that in two sites unburnt for many years, numerous seedlings were growing amongst ground cover plants such as *Brachyloma daphnoides*, where there is protection and a lower light intensity than in open areas. The present cabinet trials showed optimum germination occurred in total darkness, with germination better in light values of 25% and 12.5%, than in 50% (Table 2). This was within the relative values of light readings found under the ground cover plants in most sites. The exception was an unburnt site, where readings were taken around noon, which could have accounted for the higher light readings. Since optimum germination conditions occur in total darkness, the faster germination in lower light intensities would increase the time span when conditions are more favourable for germination. The ecological benefit of this could be when a dry spring was followed by a wetter than normal summer, when seeds would germinate in conditions of longer days and shorter nights. Temperatures in summer could be lower under ground cover plants than in open ground. This may help keep seeds in the optimum temperature for *X. australis* seeds of 20/12°C (Curtis 1993, 1996). In some sites dense moss mats may insulate soil (Curtis 1993, 1996) and in early summer the moss may also lessen moisture loss, which would result in better imbibition. However, no temperature or moisture data were taken to substantiate this hypothesis.

Light inhibition of *X. australis* seeds was lessened by the presence of charcoal, charcoal solution and gibberellic acid. In the presence of gibberellic acid, the response to light of *X. australis* seeds was similar to two Western Australian species, *Xanthorrhoea preisii* and *X. gracilis*. Seeds of the former responded at 15°C and 23°C, and the latter at 15°C. Bell et al. (1995) suggested the response may be due to involvement of the light sensing pigment called phytochrome.

The presence of smoke can have a beneficial effect on seed germination of many plant species (Brown et al. 1994; Dixon et al. 1995). In Western Australia, the need to rehabilitate areas disrupted by mining has encouraged research into the effect of smoke on seed germination, but seeds of the *Xanthorrhoea* genus have not been among those studied by Dixon et al. (1995), Grant & Koch (1997) and Roche et al. (1997). However, although the presence of charcoal, both as a powder and filtrate, stimulated earlier germination of *X. australis* seeds in light and delayed it by a week in darkness (Fig. 3), it did not significantly affect the final number of germinants. It is possible that direct application of smoke might have the same result. However, the presence of gibberellic acid in light speeded up the germination rate in light but retarded germination in darkness. The presence of charcoal and charcoal filtrate had similar effect.

The germination research by Curtis (1993, 1996) and the present study has provided useful information on the management of *Xanthorrhoea australis*:

- When sowing in autumn or early spring, the seeds should be buried to a depth of 3 mm.
- For rapid germination, keep imbibed seeds in darkness at 4°C for 11 weeks before sowing.
- Viability is maintained in seeds stored at room temperature and humidity in brown paper bags for at least five years without insecticides, providing no larvae are present.
- There could be an increased germination by using a mixture of older and newer seeds because of their differences in germination in darkness and light.
- The presence of understorey species lessen light intensities which helps germination and also provides protection from grazing, particularly from rabbits. This should be considered by managers when developing burning prescriptions.

ACKNOWLEDGEMENTS

I am indebted to: Dr I. A. Staff for his support and critical comments throughout this study; Drs P. J. Keane and J. W. Morgan for their comments on the manuscript; Dr R. F. Parsons for his support of the study; Max Bartley for his technical advice and assistance; and Helen Curtis for her assistance in taking field data and proof reading.

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Manuscript received 6 September 2000
Revision accepted 21 November 2001